A SIGHT REFLEX SHOWN BY STICKLEBACKS.

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The casual observer of the aquaria of the United States Fish Commission at Woods Hole, Mass., always evinces considerable interest in the behavior of the schools of sticklebacks (*Gasterosteus bispinosus*) which are exhibited annually, the attention being attracted by the very characteristic way in which these little fish swim about. During the summer of 1900, while at the Marine Biological Laboratory, the author made some observations bearing on these movements and extended them during the summer of 1904.[1]

In walking past the aquarium it was noticed that all the fish were oriented with the long axes parallel and that the whole school swam in a course parallel to, but in a direction opposite to that of the moving observer. When the observer stops the fish may also stop, but usually continue swimming in the same course, although at a slower rate, till they reach the end of the aquarium, where they usually remain as long as the observer is quiet. If the observer retraces his steps they again orient themselves and swim back to the other end of the aquarium. At first sight this looks like simple fright with movements limited by the walls of the aquarium, but this is not the case as the following experiments will show:

If the observer remains stationary opposite the center of the aquarium and moves some object, preferably a white one held in the hand, horizontally, the little fish at once respond, show a most beautiful orientation and movement, slow and uniform, opposite to that of the moving object. This movement can be arrested at any instant, or the path of motion completely reversed by moving the light object in the opposite direction. This reversal may be produced when the fish are in the center of the aquarium and has no relation whatever to the walls of the aquarium.

[1] I wish to thank the research staff of the Fish Commission for placing the aquaria at my disposal.

In Fig. 1 the rectangle represents the face of the aquarium; the large arrows indicate the direction of the stimulating object, and the smaller arrows represent the fish, showing their orientation and direction of movement.

It makes no difference whether the moving object is anterior to the fish (*A*) or posterior (*B*), their orientation is the same. In the former case they move parallel too and toward the object, in the latter case away from it.

By getting above the aquarium it was determined that the fish react in the same way to objects moving in that plane.

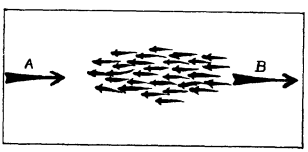

FIG. 1.

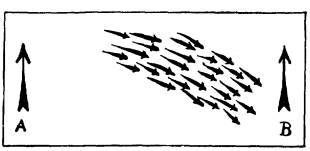

FIG. 2.

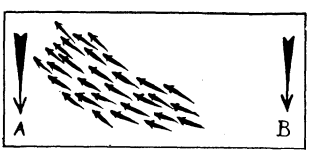

FIG. 3.

A flounder was introduced into the aquarium and swimming on the bottom beneath the sticklebacks produced the characteristic reflex.

Almost any variation of these movements may be induced by appropriate movement of the stimulating object, for example the fish can be driven from the upper right hand corner to the lower left hand corner by moving the object in the opposite direction.

By moving the object in a vertical direction the normal horizontal path can be changed up or down at will and it makes no difference whether the stimulating object is anterior or posterior to the fish. Figs. 2 and 3 show the deviation of the horizontal path.

If the stimulating object be moved slowly in this experiment the path is changed deliberately, but when the stimulus is rapid the fish may shoot in the new direction with great alacrity. A horizontal movement above the fish and at right angles to their long axes results in a deviation of their course, either to the right

or to the left, according to whether the stimulating object be moved to the left or to the right respectively. Figs. 2 and 3 illustrate this feature also, if the rectangle represent the top of the aquarium instead of its face.

By using two moving objects for the purpose of stimulation the most fascinating manouvers may be elicited. A group collected at the center of the aquarium (Fig. 4, *o*) may be broken into two platoons which move toward the ends when the stimulating objects approach the center from opposite directions. These platoons may be made to turn up or down, to face about

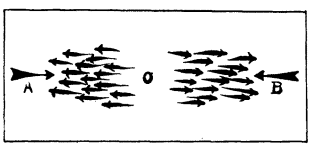

FIG. 4.

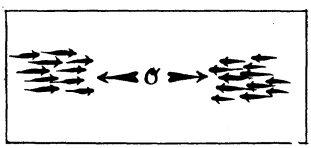

FIG. 5.

and by quickly moving the stimulating objects out from the center to charge upon one another and intermingle at the center again (Fig. 5). These reflex acts are most striking in their regularity and are executed with a military precision which never fails.

Another experiment may be performed as follows: The school of fish is brought to the center of the aquarium and the stimulating object is moved horizontally toward or away from it. In the former case some of the fish dart swiftly away to the back of the aquarium as if in fright, the others turn some to the right others to the left, thus forming two platoons as in the previous experiment, but when the object again recedes they swing about and collect in the center. In this experiment the animals which are in a direct line with the moving object are the ones to scurry away, but those outside this line are stimulated as if by some lateral change in the position of the moving body.

That there may be such an apparent lateral change can be seen by a glance at Fig. 6, in which the movement of an object from *A* to *B* has an apparent lateral motion, for example from *C* to *B* if viewed from a point outside the line of actual motion. The fish is stimulated accordingly and oriented as indicated in the diagram.

A study of the orientation of any individual fish gives the following result: When a fish is headed exactly toward the moving object a movement in any direction may be elicited, up, down, or to either side, by simply moving the object in a direction opposite to that which it is desired to make the fish take, as is indicated in Fig. 7, *a*. If the fish's long axis forms an angle with the line of motion of the stimulating object, the direction of turning in assuming its reflex orientation will depend upon which way the animal is heading. If it has somewhat the "anti"-postion with reference to the motion (Fig. 7, *b*) it will turn further into that position until its axis is parallel to the line of motion, but if it has the "homo"-position (Fig. 7, *c*) the reaction is not so certain. The fish will of course be oriented as we have already described, but it usually backs off in a hesitating way and may then turn in either direction as is indicated by the two arrows, usually however it turns in the longer arc of a circle as is indi-

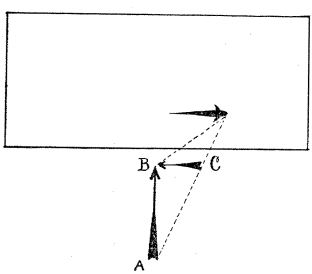

FIG. 6.

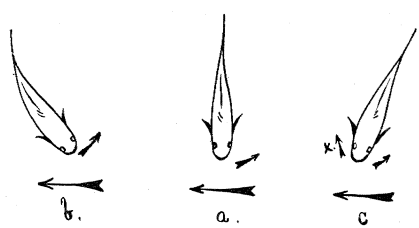

FIG. 7.

cated by the arrow at *x*, at least this is usually the case when the stimulating object is moved quickly. With a slower motion the fish usually moves through the shorter arc just as is indicated in *a* and *b*, Fig. 7.

The reactions of a number of kinds of small fish were tested among them *Fundulus margalis*, *Fundulus heteroclitus*, small eels and young sea robins, but without eliciting the reflex. Young mackerel however behaved in a manner very similar to sticklebacks, but the reactions were not so precise.[1]

[1] This reflex of sticklebacks is not invariably nor even easily obtained in small aquaria; the aquaria of the Fish Commission are about six feet long. Dr. Gaylord Clark informs me that he has tested sticklebacks for this reaction in the open water off the wharves, with positive results.

This reflex is, on the whole, most striking in its simplicity, but it is none the less puzzling for it might seem from the above experiments that the sticklebacks, and probably some other kinds of fish, form an exception to the quite general rule among animals, that by a "compensatory motion" of either the eyes, head, or whole body, the visual field is kept relatively constant.[1]

To test the validity of this view several kinds of fish were experimented with in order to determine their reactions to changes in the visual field.

1. Sticklebacks among other fish were placed in a cylindrical glass vessel which was suspended from above. Beneath and fitting quite closely about this aquarium was placed a cylindrical galvanized iron dish resting on a turn-table. The interior of this iron dish was striped alternately black and white. When this visual field was rotated the fish were very definitely oriented and swam with it, although the aquarium and water remained stationary. The fish made the compensatory effort to keep the visual field constant.

2. The animals were placed in the same cylindrical aquarium and the water set in motion by a gentle circular motion of the hand the idea being to simulate the classic turn-table experiments. As a result the animals headed up stream (rheotropism). Their efforts were materially increased by rotating the visual field opposite to the moving water, or they could be brought to rest so that they floated with the stream by rotating the field at about the speed of the moving water and in the same direction. Dr. Lyon was at the same time conducting experiments on rheotropism and by several most ingenious methods demonstrated an orientation where no current existed and where the reaction was produced only by a changing visual field.[2] Most of the fish he tested showed the same tendency to keep a constant visual field.

The results of these experiments seem at variance with those set forth in the first part of this paper, but there is this difference to be noted. The reflex depends upon a stationary visual field with the stimulating object moving before this background, a fact which offers a possible explanation of the peculiar reflex. If

[1] E. P. Lyon, *American Journal of Physiology*, 1899, III.

[2] E. P. Lyon, *American Journal of Physiology*, 1904, XII., p. 153.

we fix the eyes on any near object which is then moved, the whole visual field has an apparent motion in the opposite sense. Seated in a moving car our eyes follow the near objects as they are passed, but the *distant* landscape appears to revolve in a direction *with* the moving train. As a tentative hypothesis it may be assumed that in our experiments the moving stimulating object fixes the attention of the fish, the apparent motion of the visual field as a whole is then in a direction opposite to that of the moving object. This apparent motion may be the determining factor in causing the orientation and movement which is the essence of this peculiar reflex shown by sticklebacks.

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